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The evolution of avian parental care

Nancy Tyler Burley[1*] and Kristine Johnson[2]

[1]*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525, USA*
[2]*New Mexico Natural Heritage Program, Biology Department, University of New Mexico, Albuquerque, NM 87131, USA*

A stage model traces key behavioural tactics and life-history traits that are involved in the transition from promiscuity with no parental care, the mating system that typifies reptiles, to that typical of most birds, social monogamy with biparental care. In stage I, females assumed increasing parental investment in precocial young, female choice of mates increased, female-biased mating dispersal evolved and population sex ratios became male biased. In stage II, consortships between mating partners allowed males to attract rare social mates, provided a mechanism for paternity assessment and increased female ability to assess mate quality. In stage III, relative female scarcity enabled females to demand parental investment contributions from males having some paternity certainty. This innovation was facilitated by the nature of avian parental care; i.e. most care-giving activities can be adopted in small units. Moreover, the initial cost of care giving to males was small compared with its benefit to females. Males, however, tended to decline to assume non-partitionable, risky, or relatively costly parental activities. In stage IV, altriciality coevolved with increasing biparental care, resulting in social monogamy. Approaches for testing behavioural hypotheses are suggested.

Keywords: mating system evolution; parental care; incremental care giving; selective care giving

1. INTRODUCTION

Social monogamy with biparental care is by far the most common mating pattern among extant birds. By contrast, this pattern is rare or absent in most other taxa (Clutton-Brock 1991). This mode of reproduction was ultimately derived from an absence of reproductive bonds (promiscuity) and virtual lack of parental care, the predominant mating pattern of extant, ectothermic diapsids (lizards, snakes, crocodilians and, perhaps, turtles; Hedges & Poling 1999), the lineage from which birds evolved. We develop an evolutionary scenario that suggests how biparental care and social monogamy evolved and came to predominate among birds.

Considerable evidence indicates that birds evolved from small, carnivorous, maniraptoran dinosaurs (theropods) during the Jurassic period (Currie & Padian 1997), but some scientists believe that birds evolved from an earlier archosaur (Martin 1991; Feduccia 1996; Ligon 1999). There is continuing debate about the evolutionary relationships of extant avian orders (Cracraft 1988; Sibley & Ahlquist 1990; Hedges *et al.* 1996; Mindell *et al.* 1998; van Tuinen *et al.* 2000). Such debate makes it easy to appreciate that phylogenetic trees are hypotheses about historical affinities (Eggleton & Vane-Wright 1994), not factual descriptions thereof. Our goal is to build a coherent scenario consistent with the contemporary understanding of avian evolution but not dependent on one specific set of phylogenetic relationships. Although we note that some dinosaur traits are consistent with our

model, our scenario does not rely on the correctness of the theropod origin of birds. It is, however, dependent on the presumption of archosaurian origins.

In our scenario, biparental care evolves from female-only care. This approach contrasts with that taken by several recent authors, who propose that male-only care is ancestral among birds (Wesolowski 1994; Ligon 1999; Vehrencamp 2000). The popularity of the 'male care first' hypothesis can be traced, in part, to patterns of care observed among certain extant palaeognaths (ratites and tinamous). Although these birds are not ancestral to neognaths, it remains tempting to view their traits as the ancestral condition. Efforts to reconstruct avian history are hampered by the fact that many early avian lineages are not represented in the fossil record (Feduccia 1995; Padian & Chiappe 1998); thus, phylogenies derived from extant birds do not illuminate the origin of many avian traits deep in the Mesozoic period.

Acknowledging this limitation of current phylogenetic approaches, we note that the scenario we present below is consistent with a recent phylogenetic analysis based on three distinct phylogenies of ancestral parental care systems in birds and their relatives. Using a phylogeny in which passerines constitute the earliest avian clade, Tullberg *et al.* (2002) infer female care for the archosaurian ancestor, and a transition from female to biparental care occurs in the ancestor to all extant birds. A more traditional phylogeny with palaeognaths as basal resulted in two pathways, depending on whether character transformation was assumed to be ordered (changes in male and female care-giving states occur as separate transitions) or unordered (any change of character state is equally probable, including a simultaneous transition from no care to biparental care). The ordered assumption, which

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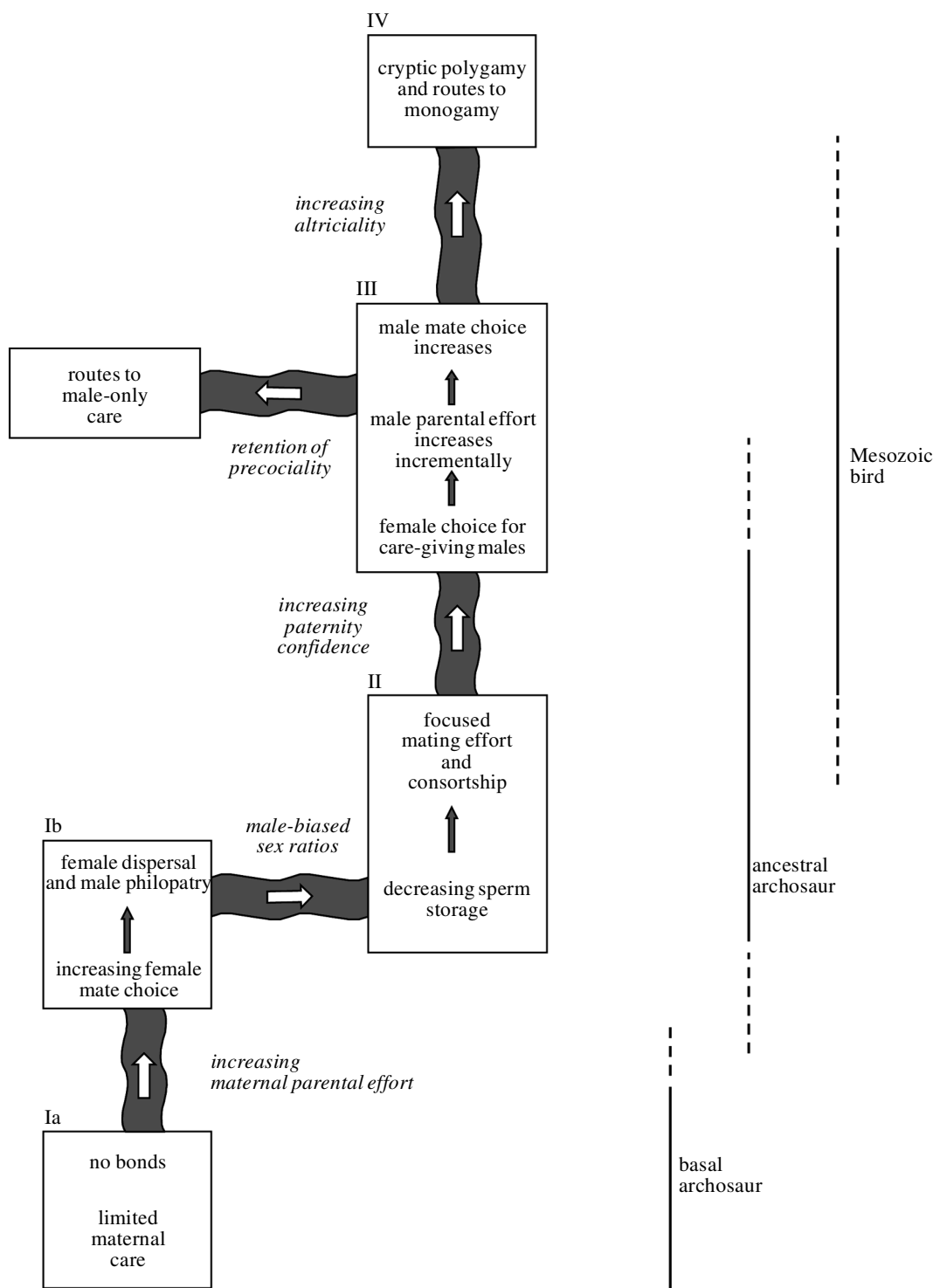DOI 10.1098/rstb.2001.0923

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Figure 1. Stage model for the evolution of parental care and mating systems in birds.

Tullberg *et al.* (2002) view as more reasonable, yields female care in the archosaurian ancestor and biparental care in the avian ancestor. If the character is assumed to be disordered, female care is inferred in the archosaurian ancestor and the state of the avian ancestor is equivocal; either female, male, or biparental care. None of the three phylogenies supports a transition from no parental care to uniparental male care. All three pathways are consistent with our view that basal archosaurs were characterized by maternal care and that biparental care evolved subsequently.

2. STAGE I: INITIAL CONDITIONS AND INCREASING MATERNAL CARE

Our starting point is a basal archosaur with a promiscuous mating system and limited maternal care, exemplified by the guarding of eggs in nests (figure 1). We select these conditions for the following empirical reasons. (i) In extant ectothermic diapsids, in which young hatch at developmentally advanced stages, parental care is rare and promiscuity is common. When care occurs, care givers (snakes, crocodilians, skinks and lizards; Bellairs 1970;

Guggisberg 1972) are almost universally female, with attendance of unhatched eggs the most common form of parental care. (ii) The young of virtually all avian species require parental care, although the extent of altriciality varies widely and rather continuously among major taxa (Starck & Ricklefs 1998). In our view, the altricial developmental types that are characteristic of neognaths must have coevolved with care-giving behaviours, simply because highly altricial young could not have survived prior to the evolution of substantial care giving.

There are two conceptual reasons to expect that female care evolved prior to male care. First is the issue of parental certainty. Early quantitative models suggesting that low confidence of paternity would not affect the assumption of parental care duties by males (Maynard Smith 1977; Grafen 1980) made simplifying assumptions, such as male inability to detect paternity and constant risk of paternity loss. More recent modelling approaches (Whittingham *et al.* 1992; Xia 1992; Westneat & Sherman 1993) and studies of birds (Parker & Burley 1997) suggest otherwise. Empirical evidence indicates that vertebrate males can sometimes assess their paternity, and under some circumstances male parental investment (the cost of parental effort for a clutch) is closely related to paternity (Owens *et al.* 1995; Johnson *et al.* 2000; Møller & Cuervo 2000; Neff & Gross 2001). The relationship between paternity certainty and paternal investment is expected to be complex, as when males with a low paternity confidence nevertheless display investment 'to make the best of a bad situation'. Nonetheless, it is unlikely that males evolved extensive parental care duties without substantial certainty of paternity (Burley & Parker 1997; Johnson & Burley 1997; see § 2d).

A second conceptual reason for expecting that female care evolved first is that the very high degrees of anisogamy exemplified by amniotes pre-adapt females for parental care. Parental care simply extends the trade-off between numbers and quality of offspring that typifies female reproductive strategies (Trivers 1972). In a promiscuous mating system with no parental care, anisogamy means that females will be the first to provide care, which in this case includes searching for a nest site, digging a hole, covering eggs and sneaking away. Before males would suddenly adopt a larger increment of parental care, such as egg guarding, they would have to receive large benefits at little cost. However, for males there is a cost that females do not experience: male fitness tends to be much more heavily influenced by the number of matings achieved (Arnold & Duval 1994). More time and effort devoted to care giving results in less availability for seeking additional mates; thus, male parental care must more than compensate for lost matings. Male-only care may readily evolve in taxa in which such a trade-off is minimal (e.g. teleosts), but we contend that this did not represent the conditions faced by basal archosaurs (see § 2d).

(a) *Additional starting conditions*

We assume an ancestral dispersion pattern whereby breeding males and females defended independent, overlapping, all-purpose territories or home ranges (Stamps 1983). Females mated with males whose territories overlapped their own. Following copulation, females stored sperm for some time before laying eggs (a month or more

is common among ectothermic diapsids; Alderton 1991) and probably mated with several males.

Females laid many small (by avian standards) eggs and buried them in moist soil or in mounds of earth and decaying vegetation. This pattern of egg deposition is found in extant crocodilians, the closest living relatives of birds, and is reported for dinosaurs, including some theropods (Mikhailov 1997). Such eggs developed slowly at ambient temperatures or slightly above ambient temperatures, if decaying vegetation provided additional warmth. Crocodilian eggs take 2–3 months to hatch (Alderton 1991). Females attended and defended their slow-to-hatch eggs, at least from small egg predators, as in some crocodilians. They may have aided hatching, as do crocodilians and a diverse array of birds.

(b) *Stage I innovations*

The near ancestors of birds were relatively small creatures with many potential Mesozoic predators. Innovations that increased offspring survival would have been especially important to the persistence of this lineage. Nearly universal avian traits that would have aided offspring survivorship include the following.

(i) Increasing egg size and/or decreasing clutch size. Increases in egg size were favoured by the greater survivorship of larger hatchlings, which were vulnerable to a smaller range of predators, vulnerable for a shorter span, or able to forage for a larger range of prey types. Increasing egg size would have resulted in a reduced clutch size (Smith & Fretwell 1974), facilitating evolution of post-hatching maternal care. It is easier to guard, herd and otherwise care for a small brood than a large brood. High rates of post-hatching depredation would have favoured the evolution of concealment and/or defence of young.

(ii) Surface nests and endothermy. Increasing egg size resulted in a longer pre-hatch interval (Ricklefs & Starck 1998*a*), but a shorter period of post-hatch vulnerability (Shine 1978). Birds display a greatly accelerated rate of embryo development due, in part, to the application of warmth during development. This accomplishment necessitated at least two innovations. One was the evolution of hard-shelled eggs exposed to air (surface nesting; Kavanau 1987). The increasing size of eggs decreased surface/volume ratios and led to numerous changes in egg characteristics (Burley & Vahedra 1989). Attacks on slow-to-hatch eggs by soil invertebrates and microbes may also have contributed to the evolution of eggshell traits and pre-adapted eggs for surface nesting (Packard & Packard 1980). Once surface nesting evolved, females were freed from the constraint of laying eggs in masses; instead, eggs could be laid over a period of several days, allowing for further increases in egg size.

The fossil record indicates that surface nests evolved early. Some dinosaur species had surface nests in which part of each egg was exposed to the air (Norell *et al.* 1995; Varricchio *et al.* 1997). *Troodon* eggs were arranged in an orderly fashion,

with the bottom half standing in sediment and the top half, containing eggshell pores, exposed.

Effective incubation required the evolution of adult endothermy. Perhaps surface nests evolved prior to the evolution of a metabolism that allows for incubation at above-ambient temperatures. Possibly, for example, females adopted behavioural adaptations, such as covering their eggs with vegetation to conceal them from predators (Kavanau 1987), and eggs continued to develop at slow temperatures. A more parsimonious possibility is that surface nests evolved after endothermy began to evolve and direct incubation by the mother increased egg development rate. Increasing egg size was an impetus to the evolution of endothermy, because moderate increases in environmental temperature would have made substantial differences in rates of egg development due to Q^{10} relationships. Additional changes in physiological control of embryonic developmental rate must have occurred eventually to permit the rapid development that is typical of modern birds, but these changes are poorly understood (Ricklefs & Starck 1998a).

Evidence regarding theropod endothermy is contradictory (Ruben 1995; Farlow *et al.* 1995; Geist & Jones 1996; Padian 1997). Some of the controversy may result from unproductive conceptual dichotomization of 'endothermy' and 'ectothermy'. It seems probable that the metabolism of modern birds was achieved incrementally rather than in one step. Our line of reasoning is consistent with the possibility that surface-nesting theropods were incipiently endothermic.

To summarize, we suggest either that surface nests co-evolved with endothermy or that endothermy and incubation greatly enhanced the usefulness of surface nesting. Once eggs were incubated, the pre-hatching span was reduced from an interval of months to weeks, decreasing losses to depredation and permitting additional increases in egg size.

During this stage, female parental investment in individual offspring gradually or sporadically increased, while males remained largely non-parental (figure 1). Females incubated and guarded clutches of eggs and herded precocial young. Males would have been likely to sire some proportion of hatchlings they encountered on their territories. Such paternity would have selected against cannibalism and might have favoured the evolution of low-cost defence of hatchlings that males encountered on their territories (noted for a few crocodilians; Alderton 1991), if such behaviour did not interfere with mate attraction and territory defence.

(iii) Mate choice and female-biased dispersal. Increasing maternal investment favoured increasing female selectivity of male traits that affect offspring quality and survival (Trivers 1972; Johnson & Burley 1997), because an increasing fraction of a female's fitness became linked to the fate of individual offspring. Selected traits included indicator traits that denote heritable aspects of vigour (Hamilton & Zuk 1982), traits favoured by aesthetic female preferences (Burley 1985; Burley & Symanski 1998) and properties of the territories in which males resided (Searcy 1979).

With endothermy, females were able to travel more widely in search of good mates. Males tolerated female intruders on their territories, because tolerant males obtained more matings. Although endothermy posed much greater energetic demands, it also greatly increased foraging abilities, allowing males to maintain larger territories. Females attending nests and broods experienced defence difficulties and began to lay their clutches on the territories of males with good defence capacities. Diffuse mating investment (Johnson & Burley 1997) by males evolved to focus on obtaining the territories most attractive to nesting females.

(c) *Dispersal and sex ratios*

As a result of increasing active female choice of males and breeding sites, females began to disperse more in search of mates, and the more sedentary, territorial males became philopatric. This sex difference in dispersal tendencies persists among most extant avian taxa (Greenwood 1980).

By the end of this stage, population sex ratios became somewhat male biased as the result of female mortality from parental investment and dispersal. (In extant, non-avian diapsids, sex ratios tend to be female biased or equal; Bellairs 1970). OSRs (Emlen & Oring 1977) were also influenced by the intermating interval. Males were available to breed throughout the mating season; females tending clutches did not mate. The high relative availability of males for mating would have contributed further to a positive feedback loop that favoured increasing female mate choice.

(d) *Alternative hypotheses*

Contrary to the above reasoning, several authors (Elzanowski 1985; Handford & Mares 1985; Van Rhijn 1990; Wesolowski 1994; Ligon 1999; Vehrencamp 2000) have recently suggested that male care evolved before female care in birds or their recent ancestors. Advocates of the male care first hypothesis tend to assume that mating systems typical of palaeognaths evolved from the condition of no parental care and that mating systems typical of neognaths derived from them, but there is no good phylogenetic support for this trajectory (Tullberg *et al.* 2002).

Arguments for the male care first hypothesis have not been presented in any detail comparable with that provided here for the 'female care first' hypothesis, and thus they cannot be inspected closely. General problems with the male care first hypothesis, however, are readily apparent. Extant archosaurs (and other care-giving diapsids) display maternal care almost exclusively: female crocodilians locate nest sites and dig nests, bury the eggs after they lay them and often attend them past hatching. Although egg production itself can be excluded as a form of care (although not as a form of parental investment), a male care first scenario would require that birds evolved from an ancestor in which females showed no preparation of the nest site or post-laying care. In the scenario sketched above, this would mean that after evolving sur-

face nesting, females acquired a tendency to abandon their freshly laid clutches, so the system reverted to 'no care'. Wesolowski (1994) argued that this reversion might have occurred because egg size had become so large as to severely tax maternal investment capacity. Males then began to guard and eventually incubate eggs, originating a new (male care first) sequence. In our view, parental care, in the form of incubation and defence of eggs, would have been necessary before very large eggs could have evolved, and selection would not have favoured females that evolved eggs so large that they had to abandon them prior to the evolution of shared (female plus male) care.

Another question is why males would have begun to guard eggs. Wesolowski (1994) suggested that males could readily do so while defending their territories. It is difficult, however, to envision how the benefits to care-giving males outweighed the costs. Costs include those that also applied to females (e.g. decreased time available for foraging), as well as reduction of time for mate searching and courtship. Benefits depend on the relatedness of offspring to the care giver and on the effectiveness of care in increasing offspring survivorship. The greater the effectiveness of care giving, however, the stronger would have been the selection against females to abandon this role. Thus, paternity certainty needed to be high to offset male costs, including the reduced opportunity to search for additional mates. Given a promiscuous mating system (lack of reproductive bonds between males and females), increasing female mobility and female capacity for multiple mating, it would not seem possible for males to have high certainty at this stage.

For certain teleosts with external fertilization, the male care first scenario is quite plausible. In fishes that have evolved male-only parental care, males defend mating territories on which females deposit eggs. Males then spawn, defend the eggs from conspecific egg predators, maintain the nest and remove decaying eggs (Ridley 1978; Gross & Sargent 1985). No incubation is required, and males are able to attract additional females, which add their eggs to the male's nest. In some species, a male's mating attractiveness is even enhanced by the presence of eggs in his nest (Unger & Sargent 1988). Thus, it appears that the costs of parental care are very low to males of such species and probably lower than the comparable costs for females.

For some fishes, protection of eggs and protection of paternity involve similar behaviours at the same place and time. For birds, however, continuous incubation of eggs and defence of a nest would compromise a male's ability to defend his territory and locate and attract additional mates. In addition, for fishes with external fertilization, protection of paternity need occur only at the nest, but sperm transfer in birds can occur at great distances from the nest. Thus, an avian male tending his nest would have limited ability to assess his paternity in subsequent clutches laid on his territory. Proponents of the male care first hypothesis need to articulate scenarios that would obviate these problems.

3. STAGE II: THE EVOLUTION OF CONSORTSHIP

There are two necessary preconditions to the evolution of appreciable male parental care: (i) that some degree of paternity certainty has been achieved; and (ii) that the costs of initial care-taking activities are small relative to the benefits accrued. In this section, we consider how some degree of paternity certainty was achieved via the evolution of consortship. We next focus on acquisition and amplification of male parental investment.

We suggest that paternity certainty increased with the evolution of consortships that were advantageous to both sexes. Consortships evolved when individual males and females spent increasing time together during courtship (i.e. prior to copulation). Possibly consortships originated when females followed males around their territories to assess both male traits and territory attributes. Females may also have gained unrestricted access to food by remaining on a given male's territory.

For males, consortship initially served as a form of focused mating investment. The longer an individual female chose to associate with a given male (instead of leaving his territory to consider alternative mates), the greater was the likelihood that his gametes would be used to produce a clutch. Thus, selection on males to increase attentiveness to females resulted in increases in the duration of consortship.

The evolution of endothermy contributed indirectly to increasing paternity confidence by reducing female sperm storage capacity (via an impact of temperature on sperm longevity). In birds, sperm storage capacity is measured in days (Birkhead & Møller 1992), rather than months. Declining sperm storage capacity reduced the interval between copulation and egg deposition, and shortened the consortship interval necessary to result in reasonable paternity of eggs laid on a territory.

Our understanding of the function of consortship differs from much of the contemporary literature, which views consortship as a period during which males physically guard their mates and thereby prevent copulations that compromise their paternity (Møller & Ninni 1998). We have rejected that perspective on the basis, in part, of evidence that avian males lack sufficient control to preclude their highly mobile mates from EPC. Instead, we view contemporary avian consortship patterns as serving multiple functions, including the assessment by males of female mating fidelity (Johnson & Burley 1997). We adopt the same perspective here for the evolution of consortship patterns: males with a strong tendency to associate closely with females during their fertile period acquired useful information concerning their paternity. Males also evolved courtship behaviours, including manipulative signals designed to influence female behaviour.

4. STAGE III: INCREMENTAL CARE GIVING AND THE EVOLUTION OF MALE PARENTAL EFFORT

By the end of stage II, males were positioned to adopt parental care activities. They enjoyed some paternity certainty, and male mating effort (time and effort devoted to mating) had become focused on individual females. In stage I, male mating effort had been diffuse; i.e. males placed effort into the development and maintenance of traits designed to be generally attractive to all females, such as secondary sexual traits and territories. By the end of stage II, males consorted with individual females for prolonged intervals. They may also have evolved courtship

feeding, another form of focused mating effort found among many birds. Once mating effort became focused on individual females, behaviours and physical traits that formerly functioned as mating effort began, increasingly, to acquire parental functions (Johnson & Burley 1997). For example, territory defence without a consorting female would constitute diffuse mating effort, whereas defence of a feeding territory on which a female consort forages and nests may be considered parental effort (time and energy devoted to a clutch of offspring). Likewise, courtship feeding or alarm calling by an unmated male could be viewed as focused mating effort, while these behaviours performed during consortship could also be favoured because they increase female egg-laying capacity and/or offspring survivorship (parental effort). Thus, consortship facilitates a shift from diffuse to focused mating effort, initiating a natural transition to male parental effort.

We propose that greater paternity certainty for consorting males, limited male parental effort and widespread female choice of mates made increasing male parental effort profitable to early birds (figure 1). We propose that this transition was initiated by female preference for males providing parental care. It was fuelled by three conditions: (i) the occurrence of male-biased sex ratios, which increased female ability to extract paternal care from their social mates (differential allocation; Burley & Calkins 1999); (ii) the fact that most forms of avian parental care can be partitioned into small units, which could then have been adopted incrementally (e.g. diurnal incubation, brooding, feeding and low-risk defence activities), which we call 'incremental care giving'; and (iii) the occurrence of a nonlinear relationship between parental effort and parental investment, in which low parental effort has little cost and high parental effort has disproportionate cost (accelerating cost; Burley 1980). Under such conditions the initial benefit to females and young of a small increment in male parental effort was greater than the cost of the increment to males (figure 2), thus providing additional incentive for male care giving.

The plausibility of accelerating cost varies among care activities. Certain activities may show a linear relationship. For example, the risk of being preyed on during incubation might be relatively constant over time, but at some point, the cost of increasing incubation duration begins to accelerate, as the incubator begins to starve. Likewise, a parent foraging for a small brood may have sufficient residual resources for its own maintenance, but as brood size increases, at some point the parent must become stressed (Burley 1980).

In summary, we propose that sustained directional selection arising from the co-occurrence of differential allocation, incremental care giving and accelerating costs resulted in significant evolutionary increases in male parental care, even though at any one time females selectively mated with males that provided amounts of care only slightly greater than the population average. As male parental effort began to increase in stage III, males displayed increasing selectivity of mates (Johnson & Burley 1997). From this point on, male, as well as female, mate choice tactics and/or criteria influenced subsequent evolutionary trajectories. Criteria of male mate choice included traits that signalled female fecundity and a capacity for invest-
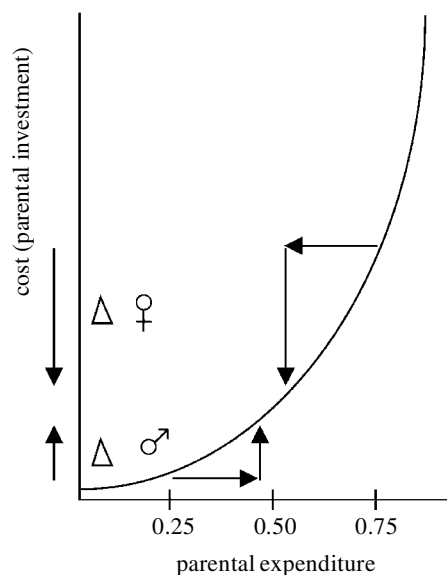

Figure 2. The relationship between parental effort and the cost (parental investment) of parental effort. Parental effort units are expressed as the proportion of effort (time and energy) needed to rear one brood. Units of parental investment are arbitrary, but increasing parental investment lowers future reproductive value. Where the difference in parental effort between the sexes is large, there is a large benefit to the higher-investing sex and a small cost to the other sex of reallocation of parental duties. As parental effort approaches 0.5, the strength of this asymmetry declines. If increasing expenditure requires qualitative shifts in behavioural strategies (Power 1980) or physiological processes, we might expect that the relationship between parental effort and parental investment is not a smooth curve, but shows abrupt changes in slope at points reflecting these shifts.

ment (condition, clutch or egg size, and good genes). Increasing male parental care permitted the evolution of high degrees of offspring altriciality, which, in birds, is associated with rapid development rates and high adult brain-to-body size ratios (Ricklefs & Starck 1998*b*). This trajectory is outlined in § 5.

5. STAGE IV: ALTRICIALITY AND CRYPTIC POLYGAMY

Here, we outline a scenario by which increasing altriciality coevolved with increasing paternal and maternal investment. A range of low-cost parental duties that could be acquired incrementally allowed for the evolution of male care. The benefits of male parental care (higher offspring survivorship and the safety net that male care provided when mothers were depredated), combined with the force of female preference for care-giving males, resulted in a positive feedback loop favouring increasing male care. Here, we suggest that increasing male parental care, in turn, facilitated the evolution of greater offspring altriciality, because the availability of two parents allowed offspring dependency to increase. Various degrees of altriciality are evident among neognaths (Starck & Ricklefs 1998), suggesting that altriciality could have evolved gradually.

Several factors might have affected the male tendency to acquire specific forms of parental care.

(i) Ability to acquire duties incrementally. The only avian parental behaviour that may be difficult to acquire incrementally is nocturnal incubation. Nocturnal incubation may be relatively expensive, both in terms of depredation risk (Ligon 1993) and physiological costs (Reinertsen 1996), especially for ground nesters. Accordingly, we expect that male birds were slower to adopt nocturnal incubation than other forms of care.

(ii) Novelty of parental behaviours. Previously, we have argued that some forms of male parental investment evolve as extensions of male mating investment. These include territory defence and feeding the female. Such parental activities should tend to evolve readily.

(iii) Benefit–cost considerations. Generally, older offspring have higher reproductive value because they have survived some period of mortality risk. In addition, they require less future investment. Thus, males may have more readily evolved extensive care giving of older offspring.

A prerequisite for the evolution of high levels of altriciality was the acquisition of nest sites affording greater protection, because the high rate of nest visitation by parents attending altricial young would have increased nest depredation rates. Accordingly, we expect that flight capacity preceded the evolution of full altriciality. Flight permitted parents to nest on cliffs or in trees, which, initially at least, would have offered greater protection from predators. The exact timing of the evolution of flight is not crucial to our scenario, provided that it appeared with or after endothermy and before altriciality.

(a) Social monogamy and equilibrium male parental investment

As male parental investment increased, males eventually became routinely constrained to social monogamy by the high parental contributions necessary for reproduction (Trivers 1972). Under the force of increasing relative male parental investment, population sex ratios declined towards 50%. OSRs also declined, because males, as well as females, became less available for mating when offspring were dependent. A logical evolutionary outcome of such pressures would be a fluctuating equilibrium at which males and females tended toward equal parental investment, with a population sex ratio hovering around 50% male. Nevertheless, several factors might have caused the sex ratio to remain male biased, and male parental investment to remain less than that of females: these include greater female dispersal, accelerating costs of increasing male parental investment, selection against adoption of high parental investment by attractive males and sex differences in costs of parental care due to sexual dimorphism or life-history differences (Reynolds & Székely 1997). In short, the advantages of increasing parental investment to males eventually declined and the costs increased, such that at equilibrium levels, male parental investment remained somewhat lower than female parental investment.

As social monogamy became more common and male mate choice increased, female access to mates became contingent on female mate quality. A general pattern of positive assortative social pairings based on mating attractiveness would have resulted (Burley 1983), and females mated to less desirable partners would have experienced increased incentive to seek additional genetic mates. The widespread pattern of social monogamy combined with persistent but variable levels of EPF resulted in the mating system we call 'cryptic polygamy' (Johnson & Burley 1997).

We suspect that much of the subsequent radiation of avian mating systems among species with altricial young (frank polygyny, promiscuity and polyandry) is derived from cryptic polygamy with biparental care. Important determinants of mating system trajectories include ecological and life-history variables; for example, after evolving extreme altriciality of offspring, some lineages subsequently adopted diets that were permissive to female-only care, and male reproductive tactics to maximize offspring numbers re-emerged. In other taxa, phylogeny has so constrained diet and life history that all representatives have retained social monogamy, and some species may have attained true monogamy. We propose that male-only care, as typified by palaeognaths, evolved from biparental care, branching off somewhere in stage III (figure 1).

6. TOWARDS HYPOTHESIS TESTING

We propose that female-only care coevolved with increasing egg size in the ancestors of birds; biparental care followed; and from biparental care, a wide radiation of mating systems has taken place. In a few relatively precocial lineages, sole male care has evolved. In some other lineages, a reversal to female-only care has occurred. Assuming the 'palaeognath-basal' phylogeny to be correct, Mesozoic birds would have achieved at least stage III of our model. Given a 'passerine-basal' phylogeny, some Mesozoic birds would have achieved stage IV of our model.

Our approach to reconstructing the evolution of parental care and mating systems of birds has been to seek to understand the life-history and behavioural options available to the ancestors of the taxon and to ask which trajectories would result in the patterns evident in contemporary birds. We can explore the validity of the behavioural options proposed by asking whether evidence has been found for similar responses in extant birds. Several tests are suggested.

(a) Sex ratios and parental investment

We have suggested that male-biased sex ratios contributed to the evolution of paternal care in birds. This hypothesis can be explored among extant birds by examining and/or manipulating local sex ratios. Within species with optional or mandatory biparental care, we would expect the average male share of care to be directly proportional to the sex ratio (males/total) of the adult population. In the first manipulative study of adult sex ratio in the socially monogamous zebrafinch (Burley & Calkins 1999), this pattern was found. This is direct experimental evidence that the sex that is in short supply can negotiate and obtain greater parental effort from the non-limiting

sex. Several studies in fishes found parental care patterns changing with sex ratio (Balshine-Earn & Earn (1998) and references therein). Further work is required to explore the generality of these responses.

(b) *Prior advantage hypotheses*

We have proposed that in a system in which only one sex provides parental care, shared care duties will evolve more readily for activities that can be partitioned into small, relatively inexpensive units (incremental care giving). In a related vein, the sex with few or no ancestral duties is likely to be more amenable to caring for older offspring with higher reproductive value (selective care giving) and will therefore tend to adopt feeding of older offspring prior to evolving care of younger offspring. Both of these hypotheses are based on the idea that evolving biparental care from uniparental care involves a series of 'bargaining sessions' in which the sex without prior parental investment or with substantially lower parental investment has greater control over which activities to adopt (other things being equal). The sex with greater prior parental investment should accept any increment of helpful care.

Extant lineages may have radiated from (in some cases relatively 'recent') ancestors that showed male-only care, female-care, or biparental care. Within extant lineages showing biparental care, but in which female-only care is known to be ancestral, we expect that male care-giving activities tend to increase as offspring age. When male-only care is ancestral, the reciprocal pattern should be found. We also expect that nocturnal incubation will be performed by the sex that ancestrally had sole care of the young.

When females provide appreciably more care than males, manipulation of the costs of care to females (e.g. by adding weights or trimming flight feathers) should result in proportionately greater increases in late male care than in early male care. The sex with greater average care should show a greater tendency to stay and care for young (versus abandoning the brood) if the other parent is experimentally removed; the discrepancy between the sexes in their tendency to abandon following the loss of a mate should diminish as the young mature.

(c) *Accelerating costs*

In contrast to experiments that manipulate costs of care to females, experiments that alter adult sex ratios to make females more limiting should elicit increases of relatively costly or early care by males (but not necessarily the acquisition of behaviours not usually displayed by males), at least when multiple nesting attempts are possible within a given season. This is expected because male remating opportunities are low relative to those of females, thus giving females the ability to demand substantial increases of male parental investment. In order to investigate this possibility, it would be necessary to establish, using physiological techniques, which parental behaviours have costs that accelerate most rapidly with increasing parental effort. Females should be more likely to abandon mates that fail to take on substantial increases in parental investment (in response to altered sex ratios) than those that do increase their parental investment.

7. CLOSING THOUGHTS

At present, there is a surge of interest in applying phylogenetic analysis to questions of social evolution. A potential pitfall of this approach is that ancient processes or origins cannot reasonably be inferred from relatively recent patterns. For example, several studies have shown that recent transitions from male or biparental care to female offspring care have occurred more commonly than transitions from female care to other care-giving states in lineages of fishes and some birds (Gittleman 1981; Goodwin *et al.* 1998; Reynolds *et al.* 2002). From this pattern it is tempting to infer that female-only care is an evolutionary dead end, and that male care therefore must have been the first care-giving state (arising from no care, and sometimes leading to biparental or female-only care). This is an example of the inferential fallacy (Alker 1969), as can be appreciated by simple analogy. Flightlessness has evolved from flight several times in recent avian lineages, but the reverse has not occurred. Does this mean flight cannot evolve from flightlessness? Of course not! Rather, it means that such an evolutionary step is intrinsically unpredictable. Thus, we cannot illuminate the origins of taxa by analysing patterns of persistence or change in their descendants millions of years later, and we must exercise caution in the inference from patterns produced by phylogenetic analysis.

Another important topic involving questions of scale and inference is the role of ecology in mating system evolution. In recent decades, behavioural ecologists have sought to find ecological determinants for the diversification of animal mating systems and have tended to minimize the importance of other variables, such as behaviour and (until recently) history. We believe this approach is often insufficient to explain larger patterns (Arnold & Owens 1998). Certainly, the Mesozoic environment had to have been permissive to the evolution of birds, and certainly some aspects of it (e.g. depredation on eggs and young) were important in shaping their evolution. But it would be short sighted to attempt to explain mating system evolution purely on the basis of simple ecological or historical variables. We need to include behavioural innovations that may influence evolutionary trajectories (West-Eberhard 1983), and we need to develop a framework for the logical assessment of ideas in the light of current theory. This paper reflects our attempt to apply such a perspective to the evolution of avian mating systems. We hope that this approach will stimulate future researchers to further develop and test the ideas presented.

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